Adaptive Networks for Restoration Ecology

Rafael L. G. Raimundo[1,2], Paulo R. Guimarães Jr[2] and Darren M. Evans[3]

[1] Laboratório de Ecologia Animal, Departamento de Engenharia e Meio Ambiente, Centro de Ciências Aplicadas e Educação, Universidade Federal da Paraíba, Campus IV, Rio Tinto, PB, Brazil.

[2] Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil.

[3] School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, United Kingdom.

Corresponding author: Rafael L. G. Raimundo (rafael.raimundo@ccae.ufpb.br).

The urgent need to restore biodiversity and ecosystem functioning challenges Ecology as a predictive science. Restoration Ecology would benefit from evolutionary principles embedded within a framework that combines adaptive network models and the phylogenetic structure of ecological interactions. Adaptive network models capture feedbacks between trait evolution, species abundances and interactions to explain resilience and functional diversity within communities. Phylogenetically-structured network data, increasingly available via Next-Generation Sequencing, inform constraints affecting interaction rewiring. Combined, these approaches can predict eco-evolutionary changes triggered by community manipulation practices, such as translocations and eradications of invasive species. We discuss theoretical and methodological opportunities to bridge network models and data from restoration projects and propose how this can be applied to the functional restoration of ecological interactions.

Keywords: Anthropocene, big data, coevolution, environmental DNA, prestoration.

Glossary

Biodiversity big data: large datasets provided by a variety of sources, such as field surveys and Next-Generation Sequencing technologies (e.g., environmental DNA), that can be used to describe ecological populations and communities [1].

Coevolutionary dynamics: the processes of local adaptation mediated by reciprocal natural selection between interacting species [2]

Ecosystem functions: biological and geochemical processes that govern biodiversity organization and the flow of matter and energy across ecosystems.

Ecosystem services: outcomes of ecosystem functions that have socio-economic value, such as crop pollination and pest control.

Forbidden links: interspecific interactions that do not occur due to trait incompatibilities of potentially interacting individuals, such as mismatching morphologies or phenologies [3].

Functional diversity: "the range and value of those species and organismal traits that influence ecosystem functioning" [4], a notion that relates to the extent to which species are functionally complementary (functional complementarity) or redundant (functionary redundancy).

Interaction rewiring: the reconfiguration of an ecological network arising from the establishment or cessation of pairwise interactions as a consequence of adaptive or stochastic processes.

Next Generation Sequencing (NGS): several novel techniques that allow the rapid, inexpensive, and genome-wide sequencing of DNA. These can be used to construct large, phylogenetically-structured species-interaction networks [5].

Resilience: the extent to which an ecological system absorbs disturbances without fundamental changes in its structure, dynamics, and feedbacks [6,7].

Robustness: the "ability of a system to maintain itself within a narrow range of function" [8].

Rewiring rules: algorithms used to model the processes that drive interaction rewiring.

Stability: the ability of an ecological community to buffer disturbances and return to an equilibrium point after a small perturbation of population densities [9].

Topological roles: the patterns of interaction of a species within a network with regards to how its interactions are distributed within and among cohesive species groups, the so-called modules [10].

Restoration Ecology: developing the application of ecological networks

With unprecedented biodiversity losses as a result of anthropogenic disturbance, restoration of many ecosystems is needed to re-establish the provision of valuable **ecosystem services** (see **Glossary**) [11, 12]. Historically, Restoration Ecology has applied ecological theory to recover biodiversity and **ecosystem functions** [12]. Recent theoretical advances provide new ways to consider the restoration of community properties, such as **resilience** and **functional diversity** [13]. One such perspective is the ecological network approach to restoration, which benefits from a growing understanding of how species-interactions affect community organization and dynamics [14]. Several studies show how ecological networks can link new ways of understanding and planning ecosystem management [13,15,16].

Ecological networks can be powerful tools for restoration because species-interactions shape, and are shaped by, ecological and evolutionary processes that maintain biodiversity and its related ecosystem functions [17]. Networks are already used to provide informative assessments of restoration outcomes [13]. For example, the removal of invasive species from a plant-pollinator network has been shown to increase the number of interactions per species, which in turn enhanced pollination quality and functional diversity [16]. Importantly, networks can also be used to plan and better predict restoration outcomes [13, 15,16].

The potential of using network models for restoration has been strengthened by novel sources of **biodiversity big data**, such as those created through **Next Generation Sequencing (NGS)** technologies that provide unprecedented amounts of information on species-interactions, including their phylogenetic-structure, in a cost-effective manner [1,5]. For example, 'nested tagging' DNA-metabarcoding

approaches can create highly-resolved host-parasitoid networks using >1000 insect hosts in a single sequencing run [18]. We contend that using phylogenetically-structured species-interaction data to inform dynamic network models is a major advance linking theoretical and applied research to support and predict the outcome of restoration strategies.

The manipulation of community composition is one pivotal aspect of restoration practices, which routinely add or remove species from communities, such as in species translocations (e.g. [20]) and in the eradication of invasive species (e.g. [21]). Network models can help to inform the selection of species to be added or removed by considering, for example, the expected outcomes under variable degrees of perturbations [22] or alternative restoration targets [15]. In order to improve the usefulness of ecological networks for restoration, we show that these can readily incorporate evolutionary principles, which to date have mostly been overlooked.

Eco-evolutionary network models using phylogenetically-structured species-interaction data can help to predict how the manipulation of community composition reshapes its resilience, **stability** and functional diversity - key properties for setting restoration targets and biomonitoring assessment. Here, we (1) show that rapid evolution within ecological networks is an important consideration that is expected to affect restoration outcomes; (2) present the theoretical background that underpins a restoration framework based on adaptive networks - a general class of dynamic network models; (3) identify the steps required to merge adaptive network modeling with phylogenetically-structured species-interaction data; and (4) discuss the opportunities and challenges to bridge network models and field data generated

by restoration scientists in a mutually beneficial exchange between pure and applied researchers. Overall, we seek to stimulate integrative research on the mechanisms that drive restoration outcomes - an understanding that is fundamental for predictive restoration science [19].

Why is rapid adaptive evolution important for restoration ecology?

Restoration ecology has historically overlooked evolutionary theory [23]. Nevertheless, compelling evidence shows that the rapid evolution of functional traits (**Box 1**) can affect community dynamics [24]. Indeed, traits that mediate species interactions can evolve even within a few generations [25]. For example, body mass evolution in reed warblers (*Acrocephalus scirpaceus*) that colonized a restored wetland in Malta was recorded over a period of just 19 years [26]. Rapid trait evolution can affect life histories [27], ecological dynamics [28], and ecosystem services [29]. In turn, such ecological changes reshape the local interplay of evolutionary processes, creating feedbacks between ecological and evolutionary processes [30]. Eco-evolutionary feedbacks might influence restoration outcomes as species that lack a coevolutionary history start to interact within degraded environments, triggering rapid adaptive evolution [31]. Strong trait selection in organisms used for restoration will often be predictable, as illustrated by repetitive evolution of small plants and seeds, and earlier flowering, in the grass *Elymus elymoides* ssp. *californicus* after post-fire restoration [32].

We next introduce adaptive network models (ANMs, **Box 2**, see [33]) to show how they can incorporate eco-evolutionary feedbacks to support ecological restoration strategies.

Box 1. Rapid evolution, ecological dynamics, and the restoration of seed dispersal networks

Ecological interactions link selection and population dynamics and account for ecological and evolutionary processes driving biodiversity. The subset of organisms bearing traits favoured by selection imposed by ecological interactions can show intrinsic growth rates that are higher than the average of the population [34]. The demographic consequences of rapid evolution on populations have repercussions on community structure [24,28] and dynamics [30].

The rapid evolution of palm tree seed sizes following the extinction of large-gaped birds in the Brazilian Atlantic Forest [35] (**Figure I**) illustrates how changes in community composition can trigger rapid evolutionary changes whose ecological effects can reshape the distribution of traits, abundances, and interactions at the community level [30,36]. In Atlantic forest fragments where these large frugivores no longer exist, palm trees now produce smaller seeds, which can negatively affect seedling survival [35]. Accordingly, rapid trait evolution in human-modified environments can have broad effects on ecosystem functions, as illustrated by the seed dispersal deficit imposed by the evolution of smaller body sizes of frugivore fish species due to selective fishing [29].

Community manipulation for restoration purposes will often trigger feedbacks between trait evolution and population dynamics [31]. Understanding how such feedbacks change network structure [36] is relevant, for example, to support decision-making regarding whether to introduce or eradicate species for restoration. Similarly, the restoration of seed dispersal networks within Atlantic Forest fragments subject to defaunation [35] requires a predictive framework for the selection of frugivorous species whose reintroductions can recover the interactions of species that have lost their seed dispersers.

How can adaptive network models (ANMs) be used in restoration research?

ANMs are part of the ongoing integration of ecological and evolutionary theories of community dynamics, which include eco-evolutionary dynamics [30], evolutionary metacommunity theory [37] and the geographic mosaic theory of coevolution [2]. ANMs capture eco-evolutionary feedbacks that connect community-

level dynamics of ecological interactions to the population-level processes that shape species abundances and trait evolution [33,36] (see Box 2). Within a restoration context, such trait-abundance-interaction feedbacks [36] can occur, for example, when selection favours taller individuals within a plant population: as the mean plant height increases, the population sizes of herbivores also increases due to higher food availability, triggering the adaptive evolution of novel forms of plant resistance (see [31]) and ultimately changing the interaction patterns at the community level.

Box 2. Adaptive network models: definition and application to restoration

Adaptive network models are a class of network models that incorporate feedbacks between patterns of interaction among elements (e.g., species) and the properties of these elements (e.g., species traits and abundances)[33,38]. Thus, when depicting ecological communities, ANMs capture trait-abundance-interaction feedbacks [36] (**Figure II.A**). Traits and abundances shape patterns of interaction because traits allow interactions to occur and abundances affect the encounter rates of potentially interacting species [36]. Patterns of interactions have eco-evolutionary effects that shape abundances and traits within populations. When one species rewires its interactions, the arising demographic and evolutionary effects can spread across the network via indirect interactions [28]. As a consequence, the community-level distribution of traits and species abundances will change, and further rewiring can be triggered.

ANMs account for the feedback loop between: (i) the *dynamics of networks*, which refers to temporal variation in the network structure due to interaction rewiring; and (ii) the *dynamics on networks*, which refers to changes in population-level properties of the species that form the network, such as mean traits and abundances (see [33,38], **Figure II.B**). ANMs can explore the relative roles of candidate mechanisms that produce biodiversity patterns, such as neutral and niche-based processes which can influence patterns of interaction among species [39]. ANMs can

provide testable predictions for changes in biodiversity arising from restoration practices that add or remove species from communities and refer to: (i) network structure, which is a proxy for resilience (*sensu* [6]); (ii) the distribution of species abundances, which relates to stability (*sensu* [9]); and (iii) the community-level distribution of traits, which relates to both robustness (*sensu* [8]) and functional diversity (e.g. [40]). As a simple example, the rewilding of seed dispersal networks with highly generalist animals might increase the number of interactions per species and ensure the persistence of plant species with a wide range of seed sizes (**Figure II.C**). Alternatively, the addition of a specialist plant species that connects only particular groups of highly interactive species (modules) within the network might increase modularity, promote trait divergence between unconnected network modules, and ultimately lead to the functional extinction of disconnected species (**Figure II.D**). Taken together, predictions provided by ANMs for the outcomes of community manipulation strategies can represent a broad support for the restoration of resilient and functionally diverse ecological networks.

Knowledge gaps and emerging research directions

Restoration of biodiversity structure: timescales and dynamics of interaction rewiring

Different types of ecological networks can be seen as building blocks of restoration strategies because they correspond to complementary ecosystem processes (**Figure 1**). For example, in oceanic islands, the taxonomic disparity between pollinators (mostly invertebrates, such as bees and beetles) and seed dispersers (mostly vertebrates, such as birds, bats and lizards) requires compatible restoration strategies at distinct spatio-temporal scales; the small-scale and rapid restoration of plant populations and their pollinators can later benefit from the restoration of seed dispersal interactions at broader spatio-temporal scales, which in turn will increase the genetic diversity of previously restored plant populations [41]. The restoration of such “networks of networks” [42] is a promising perspective, but

currently we still need to understand the mechanisms of **interaction rewiring** that are relevant for the restoration of particular ecological networks. The incorporation of realistic rewiring mechanisms [43,44] into ANMs can help to predict when a restored ecological network will be able to absorb perturbations by the reconfiguration of its interaction patterns (Box 2) without changes to ecosystem functioning [7].

The tempo and mode of rewiring mechanisms are expected to vary between different types of ecological interactions across taxa and ecosystems (Figure 1). Hence, the design of rewiring algorithms should take into account similarities and dissimilarities of network dynamics expected from coevolutionary history, which may be partially encoded in the phylogenetic structure of ecological interactions [45,46], to inform restoration strategies. To date, ANMs have overlooked the role of phylogeny in rewiring dynamics (but see [47]). Instead, **rewiring rules** have applied several heuristic criteria, such as the optimization of species abundances [48], the number of interactions per species and phenotypic similarity [43]. We propose that incorporating phylogenetic data and natural history knowledge into ANMs will help in predicting the outcomes of restoration practices, especially if in association with other constraints that shape network structure, such as **forbidden links** [3]. Ultimately, constraints to interaction rewiring might depend on the extent to which phylogenetic relatedness (i.e., phylogenetic signal) predicts interaction patterns [45,49]. Therefore, whenever phylogenetic signal matters, phylogenies will be helpful to inform rewiring models on which interactions are likely or unlikely to occur.

Phylogenetic signals are expected to be pervasive in reciprocally specialised mutualistic interactions, such as those between figs (*Ficus* spp.) and fig wasps (Hymenoptera: Chalcidoidea), as their co-diversification history tightly connects species, and hence rewiring events are phylogenetically constrained [50]. Indeed, strong phylogenetic constraints on interaction rewiring partially explain the modular structure of many mutualistic networks (Figure 1G, [51,52]). Phylogenetic constraints also affect network dynamics in antagonisms, for example, limiting the range of plant species used by herbivores [47]. Phylogeny is expected to constrain network structure even in generalized ecological interactions, as illustrated by a study showing that phylogenetically related species tend to interact with similar partners in 42.7% of the 105 mutualistic networks considered [45]. Although phylogenetic signals are ubiquitous in ecological networks, their strengths vary across interaction types, species sets and components of network structure [46]. Finally, in some generalized interactions, such as seed dispersal mutualisms, rewiring rarely requires further specializations [53]. In these interactions, the phylogenetic signal might be weak and selection should favour unconstrained interaction rewiring as individuals optimize their foraging strategies to face the spatio-temporal heterogeneity in resource availability [54].

Restoration of ecosystem functions: dynamics of abundances and traits on networks

Although changes in species abundances and traits are intertwined with trait-abundance-interaction feedbacks [36] (Box 2), most ANMs to date have explored ecological or evolutionary dynamics independently. The ecological dynamics of abundances on networks has been studied for decades [9]. On the other hand, we

are only just beginning to understand how networks affect trait evolution. Models of coevolutionary networks show how selection and other mechanisms shape trait evolution underpinning network structure [55,56]. For example, coevolutionary convergence, i.e., the evolution of similar traits in phylogenetically unrelated species as a result of selection arising from ecological interactions, reinforces functional redundancy by increasing trait similarity among species [57]. Therefore, coevolutionary convergence might positively affect the resilience and **robustness** of ecosystem functions, such as pollination or seed dispersal. Another example of how coevolution on networks might influence ecosystem functioning is the addition of super-generalists to pollination networks. This is expected to enhance trait matching between plants and pollinators [56], which, in turn, enhances pollination quality [58]. For antagonisms, ANMs of host-parasite interactions predict that network structure shapes, and is shaped by, selection, with transient arms races being the prevalent **coevolutionary dynamics** driving trait diversity [59]. More generally, eco-evolutionary processes triggered by frequency-dependent selection shape genetic diversity, network dynamics, and adaptive diversification [60–62]. Despite such relevance, the ecological and socio-economic consequences of rapid evolution on networks remain largely unexplored (but see [2]). ANMs that incorporate both ecological dynamics and trait evolution are likely to better predict how species additions and removals will affect restoration outcomes. Such an integrative step requires the joint efforts of theoreticians and restoration ecologists to build an ANM approach to “prestoration” [63], i.e., the selection of species sets to ensure that the restored network structure and related ecosystem functions will persist over time.

Bridging adaptive network theory and experimental restoration research

Network models can predict which subsets of candidate species can be added to a network to improve its resilience [22] or whether (and which) invasive species should be eradicated to favour the persistence of species and interactions [64]. For example, network models suggest that the consequences of species additions depend on their specialization and on the extent to which introduced species compete for interactions [65]. Simulations also suggest that introducing many generalist species can prevent network collapse [22]. Regarding species removals, models suggest that the eradication of highly connected non-native species from plant-pollinator assemblages can increase extinctions driven by ecological dynamics [66]. Together, these results support the concept that species **topological roles** within networks (e.g., network 'hubs' that connect multiple modules, see [10]) are relevant for the selection of species that will persist together in the long term. A challenge to consider is that both species roles and network properties change as species rewire their interactions. For example, in species removal simulations, the vulnerability of plant-pollinator networks to secondary extinctions decreases if species rewire interactions following the extinction of their mutualistic partners [44]. Again, predictions derived from ANMs can help to unravel the consequences of interaction rewiring for restoration, whilst simultaneously informing prestoration strategies.

A framework that combines ANMs, phylogenetically-structured species-interaction data and biodiversity monitoring (**Figure 2**) can improve network approaches to predictive restoration in several ways. First, it can improve network data completeness as conventional network sampling, based on field observations,

often misses species and interactions (**Figure 2A**). NGS cost-effectively enhances species-interaction data completeness and, moreover, provides information on the phylogenetic structures of ecological networks (**Figure 2B**). Second, ANMs can be immediately parameterized to assess predictions by combining data provided by NGS plus a variety of existing data on species abundances, trait distributions and patterns of interactions (**Figure 2C**). Phylogenetically-structured network data can improve network rewiring rules by incorporating evolutionary constraints on network dynamics. This requires the development of new methods to allow the assignment of rewiring probabilities based on different components of phylogenetic signals [46], forbidden links [3] and trait matching [67].

Phylogenetically-informed ANMs can predict the outcomes of species additions and removals in terms of resilience, stability, and functional diversity via the integrative modelling of the dynamics of species abundances (**Figure 2D**, see [48]) and trait evolution [56,59]. Once a baseline ANM is defined for a focal community, simulations of species additions or removals, such as the eradication of invasive species (**Figure 2E**), can be used to predict changes in the distribution of interactions, abundances, and traits (**Figure 2F**). Our example in Figure 2 refers to the eradication of an invasive species, but a similar approach can predict structural and functional outcomes of adding species with contrasting topological roles. We suggest that plant-insect networks are ideal study-systems to begin the operationalization of the framework because they: (i) encompass a wide variety of complementary ecosystem functions and services; (ii) have well known structural patterns that represent references for restoration targets; and (iii) have been well studied from ecological and evolutionary perspectives. Moreover, due to their short

lifespans, many insect and plant species are suitable for monitoring trait evolution, which is a key but challenging aspect of empirically assessing predictions of changes in functional diversity within restoration contexts.

Challenges and ways forward

We argue that merging the evolutionary ecology of species-interaction networks [17], modelling [33, 38], molecular techniques [5] and novel biomonitoring methods [1,18] can predict how restoration strategies will affect resilience and functional diversity (Figure 2). ANMs provide predictions to improve the functional restoration of ecological networks. In turn, data from restoration projects can validate predictions, assess modelling assumptions, and inform parameterization [68]. Improved models can then guide field trials to elucidate eco-evolutionary mechanisms driving resilience and functional diversity within restored networks. The success of this framework depends upon collaborations between network and restoration ecologists. We see this as a two-way street between theory and practice resulting in mutually beneficial partnerships. However, there are still several theoretical and methodological bottlenecks to overcome.

Overcoming theoretical bottlenecks and methodological issues

We identify three interlinked challenges to overcome in order for adaptive networks to be successful in restoration (Figure 3). First, evolutionary and ecological dynamics need to be merged into ANMs to elucidate trait-abundance-interaction feedbacks [36], particularly when considering species additions and removals within communities. This is achievable, as ANMs have already been used to model

ecological [e.g., 48] and evolutionary dynamics [e.g., 59] independently. Second, work is needed to translate phylogenetically-structured network data into rewiring rules driving ANM dynamics (Figure 3). Although studies on phylogenetic signals in ecological networks [46], mechanisms driving forbidden links [3] and linkage rules across different types of species-interactions [67] provide a starting point, a general synthesis is needed. Third, the success of this approach requires new, mutually beneficial collaborations between network scientists and restoration ecologists. The funding of co-designed, long-term restoration experiments and the systematic monitoring of species-interactions is key (Figure 3). Persuading restoration scientists and practitioners, who are likely to be operating on limited budgets and facing urgent decisions, of the benefits of using ANMs is achievable through improved communication. With the growth of field-based NGS technology and specific development of network analysis software, it will not be long before these challenges are resolved and adaptive networks become mainstream in Restoration Ecology.

Achievable benefits of using adaptive networks for restoration research and practices

ANMs can help restoration planning because they can infer the structure and dynamics of ecological networks even in the absence of detailed information [9,69]. Ideally, however, the better the description of the system, the better the inferences for restoration. The collection and standardisation of long-term abundance and interaction data to inform ANMs requires only small modifications to existing sampling and biomonitoring protocols [1]. NGS techniques can complement network data with a balance between financial costs - which are continuously decreasing -

and the expected scientific benefits (Figure 3). Concomitantly, trait-based metrics used in restoration (e.g. [70]) can be used in trait-evolution models to predict changes in functional diversity.

The ANM framework can improve the efficiency of restoration practices in several ways. For example, it should be feasible to select multiple biocontrol agents with complementary topological roles whose introduction will affect invasive taxa, mitigating their deleterious impacts [23,71]. ANMs can also improve restoration planning by considering the key role of functional trait diversity for the management of invasive species, an issue that was brought to the attention of restoration ecologists over a decade ago [72]. Finally, ANMs can also extend Synthetic Biology principles [73,74] to restoration by showing, for example, when non-native species could be incorporated as novel biological elements that contribute to resilience and functional diversity [41,64,74].

In the long-term, the scaling up of ANMs to address the functional restoration of landscapes is possible, linking the spatial planning of restoration to eco-evolutionary processes at the metacommunity scale [2,37]. Habitat patches can be modeled as adaptive meta-networks defined by nodes that represent local species-interaction networks, which are linked via species' dispersal [75]. Each link within the spatial meta-network has multiple layers of information due to interspecific heterogeneity in dispersal abilities. Hence, multilayer links describe species-specific flows of individuals that connect, at the meta-community scale, the local dynamics of interactions, abundances and traits. Recent work is unravelling how the dynamics of spatial and ecological networks together shape the turnover of ecological interactions and ecosystem functioning across landscapes (e.g. [76]). The

empirical parameterization of multi-layer links that define adaptive meta-networks is straightforward, as illustrated by the application of DNA-based genotype techniques to describe the differential contribution of frugivore species to the dispersal of seeds connecting different sites [77]. The empirical description of meta-networks requires sampling effort that balances the completeness of local network structures and the availability of information for multiple sites, which can be improved by the large-scale application of NGS technologies. A further application of ANMs is the management of multi-layer ecological networks (see [78]) that takes into account feedbacks among multiple interaction types.

Together, these ideas converge with the growing notion that new syntheses, which extend existing theoretical foundations to account for eco-evolutionary feedbacks that pervade the hierarchical organization of biodiversity [e.g. 17,79], combined with biodiversity big data provided by advances in molecular ecology, are urgently required to improve ecosystem management [80]. We contend that combining ANMs with phylogenetically-structured species-interaction data provides a much needed basis for integrating ecological and evolutionary dynamics to elucidate the mechanisms driving restoration outcomes (see the **Outstanding Questions** box). This can contribute to the expansion of the decision-space of restoration practitioners, which is key to ensure the adaptation of restoration strategies into local socio-economic contexts and to enhance ecological resilience in human-dominated landscapes [81].

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Figure Captions (Main Text)

Figure 1. Distinct types of bipartite networks, such as those depicting specialized obligate mutualisms (A, C, E) or generalized facultative mutualisms (B, D, F), show contrasting structures and relate to a variety of ecosystem functions. (**A**) Mutualism between the anemonefish *Amphiprion percula* and the Magnificent sea anemone *Heteractis magnifica*. Photo by J. P. Krajewski. (**B**) Cleaning mutualisms between the Blackspotted puffer, *Arothon nigropunctatus*, and the Bluestreak cleaner wrasse, *Labroides dimidiatus*. Photo by J. P. Krajewski. **(C)** Defensive mutualisms between ants, *Azteca* cf. *alfari*, and the tree *Cecropia pachystachia*. Photo by R. B. Francini. (**D**) Defensive mutualisms between the ant *Procryptocerus* sp. and an Euphorbiaceae species with extrafloral nectaries. Photo by P. S. Oliveira. **(E)** A pollinating seed parasite, the moth *Epicephala* sp., laying eggs on flowers of the

plant *Glochidion grayanum*. Photo by D. H. Hembry. **(F)** The bee *Melipona quinquefasciata* visiting a flower of *Aspilia jolyana*. Photo by J. Vizentin-Bugoni **(G)** Specialized obligate mutualisms often form modular network patterns in which subsets of species (represented by black and white nodes) are more interconnected among themselves than with the rest of the network. **(H)** Generalized facultative mutualistic networks are frequently nested, i.e., a core of generalist species interacts with most species within the network and a periphery of specialists mostly linked to the generalist core.

Figure 2. A roadmap for the predictive restoration of ecological networks illustrated by a hypothetical case of eradicating an invasive species, the larger butterfly (i), without a direct phylogenetic relationship with the other native species that form the assemblage. (A) A conventional sampling of ecological networks often provides incomplete datasets as observational field efforts often lack species and interactions. (**B**) Next-Generation Sequencing improves network data completeness, informs the subjacent network structure and, combined with field surveys, provides additional information on the community-level distribution of traits and abundances. (**C**) Network data, improved by NGS and systematic, long-term biomonitoring, provide information for the parameterization of adaptive network models, including species abundances, trait distributions and rewiring probabilities derived from phylogenetic distances or trait-based criteria. The trait z is the phenotype that mediates interspecific interactions between animals (A) and plants (P). The symbols S and k indicate the number of species and the number of mutualistic interactions per species, respectively. (**D**) The adaptive network model is implemented as a dynamic system in which the temporal variation in species abundances is governed by the negative and positive effects of several types of ecological interactions on population sizes. The gradient of hot colors depicts the strength of the positive demographic effects imposed by each mutualistic interaction, and the gradient of cold colors represents the negative effects of interspecific competition. The diagonal represents the negative effects of intraspecific competition. **(E)** Simulated rewired system after the removal of the invasive species (i), according to phylogenetically-informed rewiring rules based on phylogenetic distances and trait-defined forbidden links. The rewiring of mutualistic interactions also reorganizes the structure of interspecific competition, which is defined as the overlap in resource use between species within the same trophic level. (**F**) Predictions for the distributions of interactions, abundances

and traits after the removal of the invasive species (i). In this hypothetical example, the removal of the invasive species led to competitive release and interaction rewiring within phylogenetically defined modules, resulting in within-module trait convergence, decreased trait diversity at the community level, and changes in abundances and in the number of interactions per species. The ecological traits that mediate the mutualistic interactions between animals and plants are indicated by z(A) and z(P), respectively.

Figure 3. Key challenges to be solved for the system-specific implementation of the interface between adaptive network models and field data on species traits, abundances and interactions. The partial intersections of the Venn diagram depict general goals to be achieved on the interfaces between (i) theory and modelling methods, (ii) modelling methods and field research, and (ii) field data and theory-building. The central intersection of the diagram represents the general expected result, which is the improvement of our mechanistic understanding of the eco-evolutionary processes driving the outcomes of community manipulation for restoration.

Figure Captions (Boxes)

Figure I. Effects of rapid evolution on ecological interactions. Rapid evolution led to reduced seed sizes in the *Euterpe edulis* palm, the plant depicted in both photos above, in Brazilian Atlantic Forest fragments that lost large-gaped frugivore species [35], such as **(A)** the Black-fronted Piping-guan, *Pipile jacutinga* (Cracidae). In such fragments, small frugivores, such as **(B)** the Rufous-bellied Thrush, *Turdus rufiventris* (Turdidae), became the prevalent seed dispersers of *E. edulis*. Photos by M. M. Pires.

Figure II. Adaptive networks capture the interplay of processes occurring at different levels of biological organization and can be used to predict how restoration practices will affect community-level properties. (A) Trait-abundance-interaction feedbacks capture reciprocal causality between demographic and evolutionary processes and network structure. **(B)** The *dynamics of networks* [33,38] refers to the long-term rewiring of ecological interactions that drive network structure,

whereas the *dynamics on networks* [33,38] describes changes in species abundances and traits that shape the population-level properties influencing adaptive and stochastic processes that drive network structure, closing the feedback loop. **(C)** Hypothetical example of a restoration strategy in which one generalist seed disperser is reintroduced into a local network, increasing the overall network connectivity and ensuring the persistence of plant species across the entire range of seed sizes (z_s). Here, (t1) is the original distribution of seed sizes and (t2) is the expected distribution of traits arising after the reintroduction of the generalist. The sizes of the geometric symbols are proportional to species abundances. White symbols indicate species added to the community for restoration purposes. Dashed links represent the new interactions established by reintroduced species. **(D)** Hypothetical example of restoration strategy analogous to (C), but with the introduction of a more specialist plant that connects only particular modules within the network, triggering within-module trait convergence and reducing trait diversity at the community level. The community-level decrease in trait diversity is reinforced by the functional extinction of plants with large seed sizes that will remain disconnected. See the section "Bridging adaptive network theory and experimental restoration research" for further details on predictions that can be provided by adaptive network models.

Figure I (Box 1)

Figure II (Box 2)

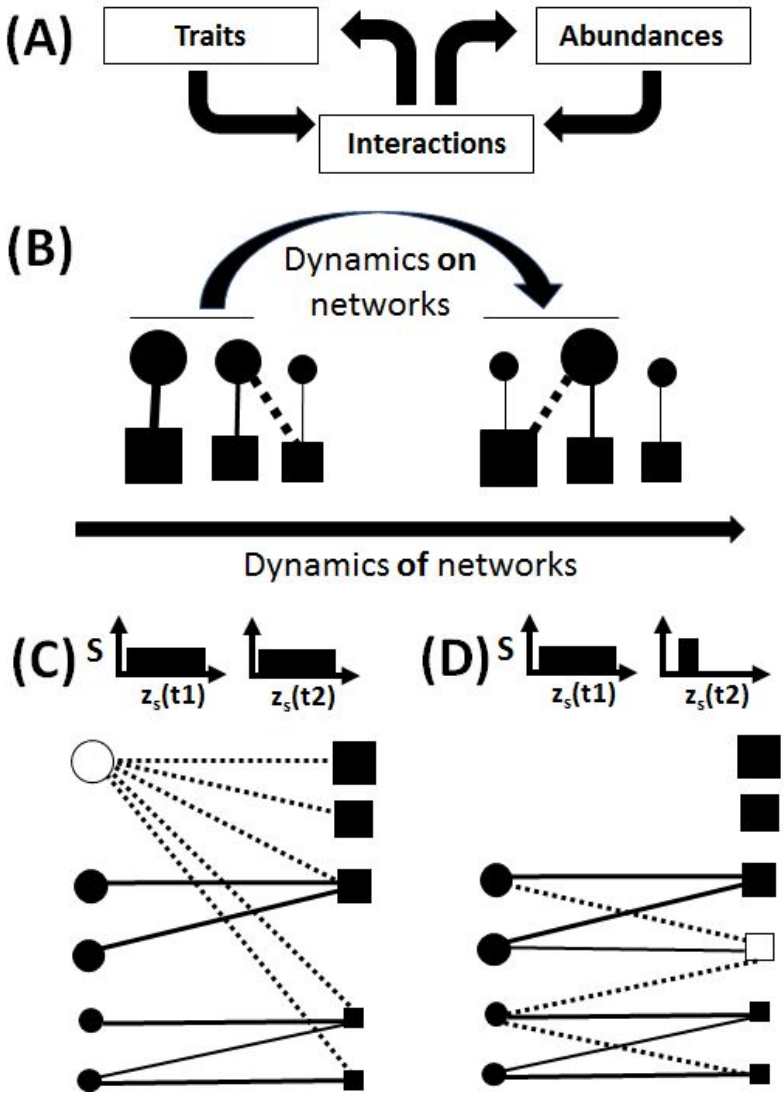


Figure 1 (Main Text)

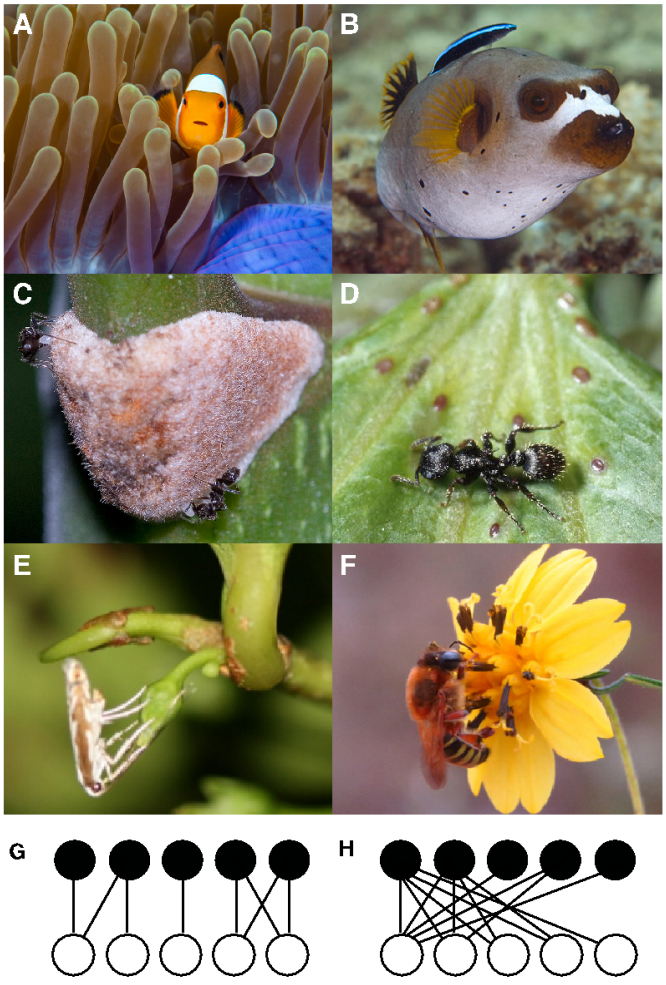


Figure 2 (Main Text)

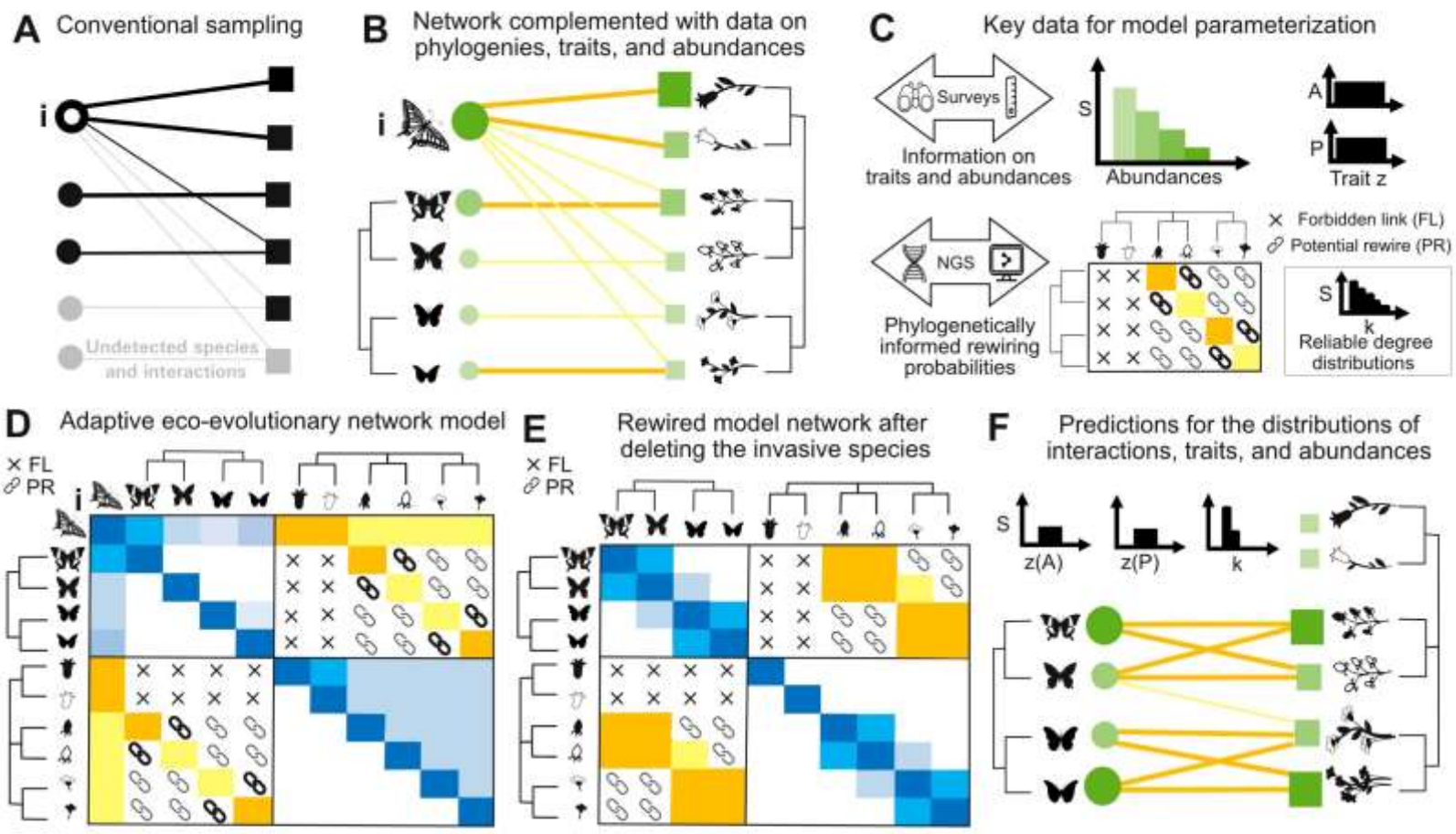
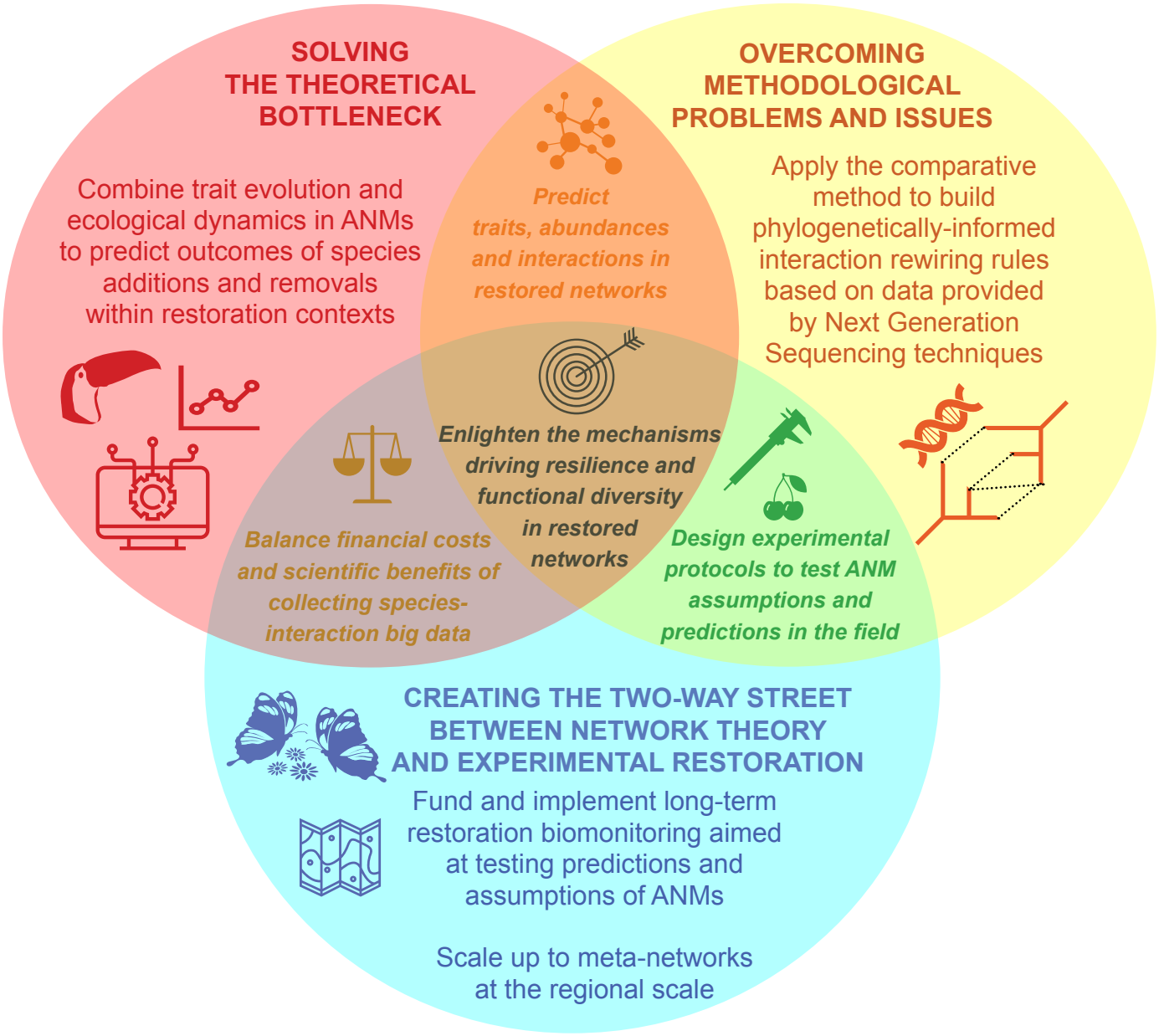


Figure 3 (Main Text)



Outstanding Questions

Adaptive network models (AMN) informed by biodiversity big data can foster novel research programs at the interface between evolutionary ecology and restoration science. Fundamental questions for the development of such an interface include: what are the effects of species introductions and removals on the organization of ecological interactions? How does the manipulation of community composition for restoration affect species traits, abundances, and ecological dynamics? How does this then impact upon natural selection in the course of ecological restoration? Evolution can change traits rapidly, but how does adaptive trait evolution propagate at the community level to redefine network structure, resilience and functional diversity? How fast is adaptive network rewiring in the course of ecological restoration and which dynamics can be expected depending on the interaction types considered?

In order to facilitate the operationalization of novel research programmes based on the ANM framework, a key methodological issue to be resolved is the application of the comparative method to translate phylogenetically-structured interaction data to inform rewiring rules. This is necessary in order to describe and understand variation in the strength of phylogenetic signals across different types of ecological interactions and its consequences for rewiring mechanisms. In many cases, phylogenetic information can promptly inform forbidden links as well as the ranges of potential interactions. Overall, a general synthesis of key concepts and methodological issues is required in order to elucidate the timescales and long-term dynamics of network rewiring over different types of ecological networks and ecosystems.

The development of models with parameters that can be easily estimated in the field, such as fundamental network metrics depicting resilience and feasible measures of trait diversity within communities, is essential for the validation of assumptions, testing predictions, and for the refinement of network models supporting predictive restoration. In the long-term, the operationalization of the ANM framework will allow us to address questions with immediate consequences for restoration practices within specific socio-economic contexts, such as: whether (and which) invasive species should be removed from native habitats and which alternative sets of interacting species could be added into communities to improve ecosystem resilience?

Highlights

- A network approach to Restoration Ecology recently emerged as a tool for integrating methodological and theoretical advances to support environmental management and decision-making.
- Adaptive network models allow us to better understand and predict how both ecological and evolutionary processes shape biodiversity and ecosystem functioning.
- In adaptive networks, the feedback between the macroscopic dynamics of interaction structure and the microscopic dynamics of population-level processes shapes interactions, abundances, and traits, hence influencing resilience and functional diversity.
- The increasing availability of phylogenetically-structured network data generated through Next Generation Sequencing techniques, alongside the standardization of biomonitoring protocols, can foster the integration of evolutionary principles into adaptive network models for ecological restoration, providing highly-resolved information for model parameterization and assessment across temporal and spatial scales.
- Phylogenetically-informed adaptive network models can be used for the selection of alternative species sets to be added or removed from communities and hence can provide flexible strategies for functional biodiversity restoration that fits local socio-economic contexts.
- Overcoming current theoretical and methodological gaps to build a two-way street between adaptive network models and experimental restoration ecology is now an achievable task, the resolution of which can broaden our ability to restore biodiversity and ecosystem functioning based on key ecological and evolutionary principles.